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Patterns in the percent sediment organic matter of arctic lakes

--Manuscript Draft--

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Abstract:	Patterns of sediment organic matter reflect the factors that affect its production and removal. We surveyed the percent sediment organic matter of 22 lakes in the Alaskan Arctic and the rate of organic matter loss with sediment age in 3 lakes in the same region. The lakes showed organic matter loss with sediment depth, consistent with the biological oxidation of organic matter. The variation in sediment organic matter among lakes was greater than the variation between shallow and deep locations within the same lake, which is consistent with landscape-scale control of variation in sediment organic matter. In sediments in shallow water, percent sediment organic matter was positively correlated with the amount of light reaching the sediments and the concentration of dissolved oxygen in the overlying water, suggesting that differences in organic matter content reflect differences in benthic photosynthesis rates. The percent organic matter of the sediments in deep water was correlated with the percent organic matter in the sediments from shallow water but not environmental variables. The results suggest that variation in sediment organic matter in this region may be influenced by variation in benthic organic matter production more than by the loss of organic matter via mineralization.
Response to Reviewers:	Dear Editor, Please find our revised manuscript (HYDR-D-15-00009). We have considered the reviewer comments carefully and have revised to manuscript to incorporate their suggestions. A detailed description of our response to each reviewer written comment is provided below in the section titled ## General Comments. The numbered entries are quoted from the reviewer comments and our response is in the un-numbered paragraph below. We have also gone through the annotations to the manuscript and incorporated those changes as needed. A description of those changes are in the section titled ## Comments in the Manuscript.

General Comments

1. "a single water column profile to define photosynthetic activity and light attenuation for the lake. This data is then compared to sediment OM that represents multiple years of accumulation. Paleolimnologists often make these time-transgressive comparisons (e.g. for paleoecological training sets), so I'm not saying the author's should remove it, but this should be acknowledged in the paper."

In accordance with the reviewer suggestion we acknowledge in the Discussion that our comparison of dissolved oxygen, transparency, and sediment organic matter is complicated by the fact that these processes vary across different time scales [lines 284 - 285].

2. Shallow and deep areas of a lake integrate very different amounts of sediment due to focusing (acknowledged in the paper L284). So in reality there are multiple timescales being directly compared between the shallow and deep cores. It's likely that the slow sediment accumulation and large sample smooths out much of the variability within the lake, which is why the deep and shallow sites are so similar. This should acknowledged somewhere in the paper.

The reviewer identifies a valid alternative explanation for the lack of variability between the sediment percent organic matter of the sediments from the shallow and deep portions of the lake. As suggested by the reviewer, we acknowledge the possibility that focusing may obscure differences between the percent organic matter of the sediments from the shallow and deep portions of the lake in our sampling in the Discussion [lines 273 - 278].

3. Dating: Are there any 137Cs results that could be used to help with the chronology? I don't think the CIC is the right model. To use the CIC model you should have a monotonic trend in 210Pb which does not appear to be the case. This is exemplified in core GTH91, where it appears that 210Pb is near background at around 6cm probably representing the 150 year limit of this radioisotope based on a half-life of 22.3 years.

We disagree with the reviewer comments on our use of the CIC model for our sediment cores. The reviewer indicates that Lake GTH 91 does not have a monotonic trend, however the exponential curve of the Pb210 activity fit to the profile from lake GTH 91 has an R2 of 0.98, which indicates that it is appropriate for the CIC model. The remaining lakes show some mixing near the surface but the model was not fit to the upper portion of the core that showed mixing. For lakes E-4 and S-3, the model has an R2 of 0.96 and 0.93 respectively. To clarify these points we indicate in the methods that the CIC model was only used for the portion of the profile that showed no evidence of mixing [line 150]. Furthermore we added the exponential model fit data to the results to provide information on the appropriateness of the model [lines 206 - 208]. Finally, we do not feel that the 137Cs is appropriate for these sediments because Cs is mobile in organic sediments and therefore would provide an unreliable peak for date estimates.

4. The dry mass accumulation rate (DMAR) is not focus-corrected. In order to compare the DMAR from one lake to another you need to account for focusing to the core site. This impacts your calculations on OM storage (L237-242 and L246-249) but probably does not impact your calculations on OM diagenesis (L233-237). To focus-correct the accumulation rates use the cumulative unsupported 210Pb flux and compare to the atmospheric 210Pb flux for the region, this is your "focus factor". For the atmospheric 210Pb flux I suggest looking at Lamborg et al (2013. Sci Tot Env 448:132-140) or contacting Dan Engstrom at the St. Croix Watershed Research Station, Science Museum or Minnesota.

We agree with the reviewer that sediment focusing could introduce some bias into our estimate of sediment accumulation rate but we do not feel that calculating the focusing factor for these lakes would add additional clarity to our estimates. Our sediment accumulation rates are based on only 2 cores from the deepest portion of the lake. As a result, we are in reality comparing one sampling site in a lake to another sampling site in another lake. In doing this, we are assuming that our sampling site is representative of the whole lake but recognize that there is error associated with the assumption. Any calculation of focusing factor would have the uncertainly associated with this assumption added to the uncertainly associated with estimating the atmospheric Pb-210 flux in the region of the lakes. Considering the magnitude of these uncertainties, we do not feel that this specific calculation would add any meaningful rigor to our estimates. To clarify this uncertainty in the paper, we added a description of the assumptions we are making to the Discussion [lines 243 - 247].

5. The ages of the cores range from 60-150 yrs. Gälman et al (2008. Limnol Oceanogr 53:1076-1082) showed that C is probably not lost much after the first 5 years following deposition. I don't think the trend in %OM you find reflects continued OM diagenesis, just variations in benthic production. Meaning I'm skeptical of the calculated OM diagenesis/loss rates (Table 3).

We certainly agree with the reviewer that patterns in organic matter with depth result from the combined effects of deposition and mineralization. On line 215 we indicate that our estimate of organic matter loss rates requires the assumption of a constant sediment accumulation rate and so we feel that we make clear the limitations of our estimate. We further develop this point when we discuss the lack of evidence of organic matter loss with depth in GTH 91 on line 261, where we acknowledge that changes in the input of organic matter to the sediments over time can affect the attribution of organic matter loss to mineralization. The reviewer cites Galman et al 2008 to indicate that organic matter is not mineralized significantly after 5 years in the sediment but we feel that the results of Galman et al are not necessarily representative of our study system. Galman et al. 2008 studied a varve lake that would be subject to much different sedimentation and mineralization patterns than the lakes in our study. Based on the organic matter content of our cores, we clearly show that organic matter was lost with depth. Since we also have sedimentation rates estimated from the 210-Pb analysis, we report the loss rate per year.

Comments in the Manuscript

Line 26 - Corrected the word order as suggested by the reviewer.

Line 28 - Replaced "photosynthesis rates" with "production" as suggested by the reviewer.

Line 59 - The reviewer questions whether a source referencing marine sediments is appropriate given that our study is in freshwater. In this statement in the manuscript we are simply defining the endpoint of organic matter mineralization on geologic time scales. We feel that given the very broad nature of the point that we are making, combined with the fact that over geologic time, there would be little difference between marine and freshwater processes, that this reference is appropriate.

Line 70 - Corrected the typo pointed out by the reviewer.

Line 149 - Our use of 210-Pb rather than 137-Cs is explained in point 3 above.

Line 174 - The reviewer questions whether the data were transformed. The data were not transformed.

Line 266 - We corrected the error in Table 1 identified by the reviewer.

Line 312 - We replaced "euphotic" with "littoral" as suggested by the reviewer. Littoral is not as technically correct but does not substantially change the meaning of the statement and is less likely to cause confusion.

Line 314 - The reviewer suggests that we evaluate the organic matter profile from Lake N-1 to support our supposition that the experimental fertilization may have created the increase in sediment organic matter in the shallow-water sediments. This was a good suggestion and the evaluation shows that it is very unlikely that the fertilization caused this increase because the difference is evident all the way to the base of the core.

	Therefore, we have removed this as a potential explanation. Line 323 - Corrected typo identified by the reviewer. Line 331 - Replaced "constrained" with "minor" as suggested by the reviewer.

Patterns in the percent sediment organic matter of arctic lakes

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LRH: Sediment organic matter in arctic lakes

RRH: K. Fortino et al.

Abstract

Patterns of sediment organic matter reflect the factors that affect its production and removal. We surveyed the percent sediment organic matter of 22 lakes in the Alaskan Arctic and the rate of organic matter loss with sediment age in 3 lakes in the same region. The lakes showed organic matter loss with sediment depth, consistent with the biological oxidation of organic matter. The variation in sediment organic matter among lakes was greater than the variation between shallow and deep locations within the same lake, which is consistent with landscape-scale control of variation in sediment organic matter. In shallow water sediments, percent sediment organic matter was positively correlated with the amount of light reaching the sediments and the concentration of dissolved oxygen in the overlying water, suggesting that differences in organic matter content reflect differences in benthic production. The percent organic matter of the sediments in deep water was correlated with the percent organic matter in the sediments from shallow water but not environmental variables. The results suggest that variation in sediment organic matter in this region may be influenced by variation in benthic organic matter production more than by the loss of organic matter via mineralization.

Keywords light attenuation; Arctic; Alaska; burial efficiency

Introduction

The anthropogenic alteration of the global carbon cycle through forest clearing and the burning of fossil fuels has highlighted the need to understand the distribution and fate of organic carbon in the world's ecosystems. Cole et al. (2007) estimate that globally, lakes store between 0.03 and 0.07 Pg of organic carbon per year in their sediments, which is 22% of the total annual carbon burial in all freshwater systems. Despite the magnitude of this pool, variation in the organic mater content of lake sediments remains incompletely characterized.

The amount of organic matter present in lake sediments results from the balance of organic matter inputs and losses. Gross primary production and detrital import increase the amount of organic matter in the system, while respiration, organic matter export, and non-biological oxidation remove organic matter (Lovett et al. 2006). However, in most lake sediments, the losses due to non-biological oxidation and fluvial export are likely minimal. In oligotrophic lakes typical of those in the Arctic, primary production is often limited. Low water column primary production results in relatively small exports of phytodetritus to the sediments (Wetzel, 2001), and production of sediment organic matter by benthic photosynthesis is limited by light availability (Stanley, 1976a; Bjork-Ramberg, 1983; Hansson, 1992; Vadeboncoeur et al. 2001; Ask et al. 2009; Karlsson et al. 2009). Only in shallow lakes with relatively large areas of illuminated sediments does benthic primary production make up a substantial component of whole lake organic matter production (Stanley, 1976b; Vadeboncoeur et al. 2008; Whalen et al. 2008; Ask et al. 2009; Karlsson et al. 2009). Thus oligotrophic lakes are generally thought to receive most of their organic matter inputs from the deposition of organic particles that wash into the lake from the watershed (Molot & Dillon, 1996).

The accumulation of sediment organic matter via primary production and allochthonous input is constantly being countered by heterotrophic respiration, which depletes sediment organic matter content (Stanley, 1976b; Ask et al. 2009). Over geologic time scales only a very small proportion of the organic matter deposited in sediments will escape mineralization (Burdige, 2007). However over shorter time scales, the rate of sediment organic matter decomposition is limited by temperature, the availability of electron acceptors (notably oxygen), and organic matter lability (Capone & Kiene, 1988; Canfield, 1994; Burdige, 2007, Fortino et al. 2014). Given the relationship between the input and destruction of sediment organic matter and environmental variables, sediment organic matter content should vary at both within-lake and landscape scales.

Landscape-scale descriptions of lake sediment organic matter content are not common in the literature and none that we know of exist for the lakes in the region surrounding Toolik Lake, but such descriptions are valuable to characterize the scale and magnitude of sediment organic matter variation. Since the organic matter content of a sediment sample will reflect the integrated effects of organic matter production, deposition and mineralization history, we hypothesized that variation in the organic matter content of the sediments of lakes surrounding Toolik Lake, AK would correlate with variation in the environmental parameters that reflect the relative rate of water-column and sediment primary production, as well as the mineralization of sediment organic matter. Using a survey of sediment organic matter from 22 lakes in the Alaskan Arctic, we evaluate the variation of sediment organic matter both within and among lakes and correlate this variation with irradiance, dissolved oxygen concentration, and dissolved organic carbon (DOC) concentration in the same lakes. Furthermore we estimate the loss of sediment organic matter with sediment depth (i.e., age) in 3 lakes to evaluate the rate of organic matter losses from sediment respiration.

Materials and Methods

Study Site

We sampled 22 small lakes (Table 1) near Toolik Lake in the Alaskan Arctic (Fig. 1). The Toolik Lake region is characteristic of the Alaskan Arctic Foothills, which is dominated by tundra vegetation and underlain by continuous permafrost (Ping et al. 1998). The annual mean air temperature is between -10^{o} and -8^{o} C and annual precipitation ranges 140 to 270 mm, of which 40% is snow (Ping et al. 1998). During the summer, air temperatures moderate to an average of 11^{o} C and the region experiences 24–h daylight (Oechel et al. 2000). The region has a complex glacial history with different aged glacial surfaces in close proximity (Hamilton 2003). Lakes E-4, EX 1, GTH 110, GTH 112, GTH 114, GTH 91, and GTH 98 are located on the older Sagavanirktok surface, which is between 780 and 125 ka (ka: thousand years before present) (Hamilton, 2003). Of these, lakes GTH 112 and EX 1 are also identified to be on deposits of windblown loess (Hamilton 2003). All of the remaining lakes except E–2, E–pond, S-3, and GTH 110 are on the younger Itkillik drift phase II drift which is between 25 and 11.5 ka Hamilton 2003). Lakes E–2 and E–pond are on the phase I drift which has an age of 120 to 55 ka (Hamilton 2003). Lake S–3 is on subglacial meltwater deposits associated with the Itkillik drift and lake GTH 110 occurs partially on the older Sagavanirktok surface and partially on solifluction deposits (Hamilton, 2003). The lake bottoms are a mixture of open mud, macrophyte beds, and cobble covered in fine sediment (Beaty et al. 2006). The open sediments are generally fine grained and organic (Table 1).

Core Sampling and Sediment Collection

Sediments were collected from open mud habitats during the summer using a K-B style gravity corer (Wildlife Supply Company, Yulee, FL). In 2007 all lakes were sampled between June 18 and June 21, except lake NE-8 and GTH 156, which were sampled on June 15 and June 27, respectively. The exact sampling date of GTH 110 was not recorded. Sediment samples were collected in the field at 1 cm increments from the top 10 cm of each core by extruding the core upwards into a basin that fit tightly over the top of the core tube. The basin permitted the capture of the highly flocculent surface sediments and had an outlet at one end that allowed for the transfer of the entire 1 cm sediment column into a pre-weighed 20 ml plastic scintillation vial. Two cores each were collected from a single "shallow" and "deep" location in each lake. The relative designations of "shallow" and "deep" refer to samples collected at the shallowest depth with sufficient sediments for coring and the deepest location in the lake. If the shallowest depth suitable for coring and the maximum depth of the lake were similar, only a single sample was collected and was designated "shallow" or "deep" based on the sample depth relative to the depth of the other lakes in the survey.

In 2008, lakes E-4, S-3 and GTH 91 were sampled in the same manner as the lakes surveyed in 2007 except that 3 replicate cores were collected from each depth and the sediments were collected into a 15 ml glass centrifuge tube. The porewater was extracted from these sediments via centrifugation (1000 or 2000 rpm for 30 min) and the sediments were transferred to glass 20 ml scintillation vials. All sediments were dried at 40 - 60º C for at least 48 h or 105º C for 12 h. The proportion of organic matter in the sediments was determined via loss on ignition (LOI) where the mass lost from the dried sediments after combustion for 4 h at 550º C was divided by the total dry mass (Wetzel & Likens, 2000). All proportions were converted to percent for analysis and presentation. Dry bulk density was determined as the dry mass the sediment of each core slice, multiplied by the volume of the core slice.

Environmental and Spatial Variables

At the same time the sediments were sampled from a lake we measured select environmental variables. We collected depth profiles of temperature and dissolved oxygen using either a YSI Model 85 multiparameter water quality meter (YSI Incorporated, Yellow Springs, OH) or Hydrolab, Data Sonde 5 (Hach Hydromet, Loveland, CO). All profiles began just below the air-water interface and measurements were collected in 0.5 m intervals to the deepest point in the lake. Photosynthetic photon flux density (PPFD) was similarly measured in 0.5 m intervals using a LI-192SA underwater 2π quantum sensor with a Li–Cor LI-250 quantum meter (Li-Cor, Lincoln, NE). The percent of the surface PPFD reaching the sediments at each depth (hereafter, percent surface irradiance) was estimated using the light attenuation coefficient calculated as the slope of the natural log of PPFD versus depth. Dissolved organic carbon (DOC) was measured from a water sample taken at the same depth as the cores using a Van Dorn sampler (Wildlife Supply Company, Yulee. FL). Samples were filtered through a 0.45 µm polypropylene (PP) filter, acidified with 500 µl of 1N HCl and stored at 4º C until analyzed for DOC on a Shimadzu TOC–V Total Carbon Analyzer (Shimadzu Scientific Instruments Columbia, MD).

^{210}Pb Analysis

Sediment accumulation rates were determined for lakes E-4, S-3, and GTH 91 using the distribution of ^{210}Pb. These lakes were chosen for sediment accumulation analysis because they have been studied much more extensively than most of the other lakes in the survey and thus, these additional data would be more valuable overall. To perform the analysis, two sediment cores were collected from the deepest location in each lake using a K-B style sediment corer. The upper 10 cm of the cores were sectioned in 1 cm intervals and dried as described above. The ^{210}Pb and ^{226}Ra measurements were made using an intrinsic germanium detector coupled to a multi-channel analyzer (Princeton Gamma-Tech HPGe, Princeton, NJ). Dried sediments were packed and sealed in gamma tubes and activities were calculated by multiplying the counts per minute by a factor (determined from standard calibrations) that includes the gamma-ray intensity and detector efficiency. Identical geometry was used for all samples. The ^{210}Pb activity was determined by the direct measurement of the 46.5 KeV gamma peak. The ^{226}Ra activity was determined following a 21 d ingrowth period via ^{214}Pb granddaughter measurement at 351.9 KeV. Accumulation rates were calculated using the constant initial concentration (CIC) model (Appleby & Oldfield, 1992) fit to the portion of the sediment profile below the surface mixed layer, if mixing was evident.

Statistics and Calculations

The mean percent organic matter content of the sediments (hereafter, mean percent organic matter) was calculated by averaging the percent organic matter in each sediment slice across the entire 10 cm core. The percent organic matter of the sediments near the sediment-water interface (hereafter, surface percent organic matter) is the average of the replicate measures of percent organic matter in the 0 - 1 cm core slice. To evaluate the general pattern of change in percent organic matter with depth, we evaluated the degree of correlation between mean and surface percent organic matter with Pearson's correlation, and tested whether surface percent organic matter was greater than mean percent organic matter in each lake using a paired t-test.

In the 3 lakes with dated sediments (i.e., E-4, S-3, and GTH 91), we estimated the rate of sediment organic matter loss with sediment depth in the deep cores by fitting a linear model (least squares) to the change in percent sediment organic matter with depth below the sediment mixing depth identified by the ^{210}Pb profile. The slope of this relationship (percent organic matter cm^{-1}) was scaled to the age of the sediments by multiplying the slope of the loss of percent organic matter with depth times the depth-based sediment accumulation rate (cm y^{-1}). Sediment age at the base of the core was determined as the mean cumulative dry mass of sediment in the core (mg cm^{-2}) divided by the mass-based sediment accumulation rate (mg cm^{-2} y^{-1}) calculated using the ^{210}Pb analysis.

Mean percent organic matter and surface percent organic matter were highly correlated (see Results) so only mean percent organic matter was used in the analysis with the environmental variables. Due to missing data, not all lakes had data for all of the environmental variables (Table 2). The relationship between mean percent organic matter and environmental variables (i.e., the lake depth from where the core was collected, percent surface irradiance, water column dissolved oxygen concentration, DOC, and temperature) were explored using pairwise Pearson's correlations. The correlations were calculated for the entire dataset and for the subset of shallow and deep samples separately. Any comparisons with a correlation coefficient greater than 0.3 were tested for significance. All analyses were performed in R (R Development Core Team, 2009)

Results

Shallow and deep samples were collected from 20 and 13 of the total 22 lakes, respectively (Table 2). The mean (± 1 standard deviation) depths of the shallow and deep samples were 2.4 (± 0.7) and 6.7 (± 2.9) m respectively (Table 2). The surface percent organic matter and the mean percent organic matter of the same core were highly correlated ($r = 0.86$, $df = 31$, $p < 0.001$). Surface percent organic matter exceeded mean percent organic matter by an average of 5.4% in a given lake and this difference occurred significantly greater than would be expected by chance ($t = 3.95$, $df = 32$, $p = 0.0004$; Fig. 2). The only lakes that did not fit this pattern were lakes S–11 and GTH 98, which had much higher percent organic matter in the sediments near the sediment-water interface than in the sediments overall (Fig. 2).

Due to the lack of suitable conditions to collect samples at both shallow and deep locations in all lakes, samples from both depths were collected in only 11 lakes (42% of the total). Within these lakes the difference between the mean percent organic matter of the shallow and deep samples ranged from -16.4 to 24.2% with a median difference of 1.5%, indicating the there was slightly greater percent organic matter in the deep samples (Fig. 3). Variation in the mean percent organic matter of the deep samples was significantly and positively correlated with variation in the mean percent organic matter of the shallow samples from the same lake ($r = 0.70$, $df = 10$, $p = 0.016$; Fig. 3). This pattern was not true for lakes N-1 and S-3 in which the mean percent organic matter of the shallow sample was much greater than that of the deep sample (Fig. 3).

Mean percent organic matter in the shallow samples was positively correlated with percent surface irradiance ($r = 0.73$, $df = 11$, $p = 0.004$) and dissolved oxygen concentration in the water above the sediments ($r = 0.74$, $df = 11$, $p = 0.006$; Fig. 4). The percent surface irradiance of the shallow samples was not correlated with the depth from which the sample was taken ($r = -0.307$, $df = 11$. $p = 0.308$), thus indicating actual differences in lake clarity and not just an artifact of sampling depth. Mean percent organic matter in the deep sediments was not significantly correlated with any of the measured environmental factors.

Sediment accumulation rates were calculated for the deep sediments of lakes E-4, S-3, and GTH 91 (Table 3). The ^{210}Pb profiles of lakes E–4 and S–3 showed evidence of sediment mixing down to 3 and

5 cm respectively but there was no evidence of mixing in lake GTH 91 (Fig. 5). The exponential decay model fits (R^2) for the unmixed portion of the ^{210}Pb profile in lakes E-4 (n = 8), S-3 (n = 6), and GTH 91 (n = 8) were 0.97, 0.93, and 0.98, respectively (Fig. 5). The deep sediments of lake E–4 are accumulating at 12.00 mg cm^{-2} y^{-1}, which is approximately twice the 6.09 mg cm^{-2} y^{-1} accumulation rate measured in lake S-3. Lake GTH 91 is intermediate with a sediment accumulation rate of 8.11 mg cm^{-2} y^{-1} (Table 3).

Below the mixing depth identified with the ^{210}Pb profile, the rate of percent organic matter loss with depth in lake E-4 (-0.99 %OM cm^{-1}) was approximately half that of lake S-3 (-2.06 %OM cm^{-1}) and there was no significant linear relationship between percent organic matter and depth in lake GTH 91 (Fig. 5). Assuming a constant sediment accumulation rate and extrapolating from sediment mass and percent organic matter profiles of the cores, in lake E-4 the 10 cm core represented approximately 62 years of accumulation and the sediments lost 0.16 percent organic matter per year (Table 3). In lake S-3 the 10 cm core represented approximately 121 years of accumulation and the sediments lost 0.17 percent organic matter per year and the sediments at 10 cm in lake GTH 91 were approximately 146 years old (Table 3).

Discussion

The percent organic matter of the shallow (1 – 10 cm) lake sediments in our survey ranged from 17.2 - 68.9%, which is bracketed by the 9 – 34% (Bretz and Whalen 2014) and 55 – 81% (Whalen et al. 2013) reported for the shallow sediments of other lakes in the region. These values generally exceed the < 20% sediment organic matter content reported for other arctic lake muddy sediments (Livingstone et al. 1958, Cornwell & Kipphut, 1992, Beaty et al. 2006). The high sediment organic matter of the surface sediments of these lakes is likely the result of low inorganic sediment inputs. The majority of the lakes in the study are located on acidic tundra underlain by permafrost (Ping 1998), which should greatly limit the input of inorganic sediment from the watershed. This observation is supported by the fact that the two lakes with the lowest mean percent organic matter (GTH 112 and EX 1; Table 2) are located on loess deposits (Hamilton 2003, Fortino et al. 2009), which would provide a source of inorganic sediment to the lakes.

Overall, surface percent organic matter was greater than mean percent organic matter (Fig. 2) indicating that there is a loss of organic matter relative to total sediment mass with sediment depth. This loss of organic matter is consistent with the biological oxidation of sediment organic matter during diagenesis. We quantified these losses in the 3 lakes with ^{210}Pb data. Our estimate of the rate of organic matter loss was similar between the two shallow lakes (E-4 and S-3) but this similarity masks differences in the estimates of sediment accumulation and organic matter loss rate. The reduction in percent organic matter with depth in the deep sediments of lake E-4 (-0.99 %OM cm^{-1}) was approximately half of what was measured in lake S-3 (-2.06 %OM cm^{-1}) but since the sediment accumulation rate in the deep sediments of lake E-4 (12.00 mg cm^{-2} y^{-1}) is approximately twice that of lake S-3 (6.09 mg cm^{-2} y^{-1}), the rates of organic matter lost per year are similar between the lakes (Table 3). Our comparison of the sediment accumulation rate among lakes contains uncertainty associated with the assumption that the two cores that we collected are representative of the sediment accumulation in the whole lake including bias introduced by sediment focusing. We did not calculate focusing factor for our lakes but sediment focusing at the site of our core collection would result in an overestimate of the sediment accumulation rate (Heathcote and Downing 2012). Nonetheless, our estimate of sediment accumulation rates are within the range of sedimentation rates (4.4 - 18.0 mg cm^{-2} y^{-1}) observed in other shallow arctic lakes (Hermanson, 1990) but were greater than the rate of 2.7 mg cm^{-2} y^{-1} estimated for nearby but larger Toolik Lake (Cornwell and Kipphut, 1992).

To estimate the amount of organic matter accumulating in the sediments in these three lakes we used the bulk density measurements to calculate that a column of sediment equal to the depth of our sampling (10 cm) would contain 727, 743, and 1274 mg cm^{-2} in lakes E-4, S-3 and GTH 91, respectively. Using the mean percent organic matter of the sediments from each of these lakes (Table 2), and the sediment accumulation times (Table 3) we estimate that respectively, lakes E-4, S-3, and GTH 91 are storing 222, 493, and 297 mg of organic matter cm^{-2} in the upper 10 cm of sediment that is accumulating at a rate of 3.6, 4.1, and 2.0 mg of organic matter cm^{-2} y^{-1}.

Interestingly, the ^{210}Pb profile of lake GTH 91 suggests that there is limited mixing of the sediments but there was no significant reduction in percent sediment organic matter with depth. Evaluation of the percent organic matter profile in lake GTH 91 shows that the organic matter content of the sediments does not decrease linearly below 4 cm (Fig. 5). Interpreting the loss of sediment organic matter with sediment age as evidence of biological activity assumes that the input of organic matter to the sediments has remained constant over the age of the core. It is possible that there has been a reduction in the accumulation of organic matter in more recent sediments that has obscured patterns produced by biological oxidation.

The shallow sediments of lakes S-11 and GTH 98 have much higher surface percent organic matter than mean percent organic matter (Fig. 2). Our data do not suggest any biological or physical reason why these lakes do not conform to the patterns seen in the other lakes in the dataset, thus we cannot speculate on mechanisms for their uncommon pattern other than to note that under certain conditions the surface sediments of Arctic lakes may differ dramatically from sediments deeper in the sediment column.

Sediment percent organic matter varied mainly among lakes and not at different depths within a lake (Fig. 3). The similarity between the sediment percent organic matter of the shallow and deep sediments in the lake is likely due to multiple factors. Sediment focusing in the deeper portions of the lake means that shallow and deep cores represent different time scales for sediment and organic matter accumulation in the lake. The combination of this difference, the overall, slow sediment accumulation rate, and our sampling resolution may have obscured some of the variability between the shallow and deep cores within a lake. The lack of difference between the sediment percent organic matter of cores from the shallow and deep portions of the lake may also suggest that sediment organic matter varies with processes occurring at a landscape scale.

The organic matter in the lakes certainly derives from a combination of autochthonous and allochthonous sources but we found that the mean percent organic matter was correlated with the dissolved oxygen concentration of the overlying water and the percent irradiance reaching the sediment surface. We acknowledge that sediment percent organic matter, transparency, and oxygen concentration reflect processes occurring over different time scales, however the correlations that we observe suggest that variation in percent organic matter among lake sediments is affected by differences in the amount of benthic primary production. In the shallow sediments, principal indicators of photosynthesis (e.g., higher percent surface irradiance and greater dissolved oxygen in the overlying water) were correlated with greater percent organic matter (Fig. 4). Although it is possible that differences in organic matter content of the sediments are driving variation in benthic primary production (e.g., via nutrient release), we are interpreting this results as evidence that benthic primary production is supplementing other sources of organic matter to the shallow sediments, as has been seen in other systems within (Stanley, 1976a) and outside of the arctic (Ask et al. 2009). Benthic primary production in shallow arctic ponds is typically limited by light (Whalen et al. 2006) and or temperature (Stanley et al. 1976b), not nutrients, and therefore should not be affected by variation in sediment organic matter content.

Despite the absence of benthic photosynthesis in the sediments below the photic zone, variation in the percent organic matter of the deep sediments also may be affected by variation in benthic primary production in the shallow portions of the lake. There was a significant positive correlation between the organic matter content of the shallow and deep sediments and in most of the lakes the percent organic matter of the deep sediments was greater than or approximately equal to the percent organic matter of the shallow sediments (Fig. 4). Thus the amount of organic matter observed in the deep regions of the lakes may be influenced by the redistribution of organic matter produced in the photic sediments to the deeper portions of the lake (i.e., focusing). Previous work in the region has found that the material sedimenting from the water column of shallow lakes is derived mainly from resuspended sediments and not phytoplankton biomass (Fortino et al. 2009).

The above pattern does not completely describe the behavior of lakes S-3 and N-1, which were among those with the highest percent organic matter in their sediments (Table 2). In these lakes the shallow sediments had much greater organic matter content than the deep sediments (Fig. 3). Although the overall high percent organic matter of the deep sediments in these lakes suggests that organic matter from the shallow portions of the lake are being redistributed, it appears that the build-up of organic matter in the littoral sediments exceeds the transfer of organic matter to the aphotic region of the lake by focusing. It is not clear why these highly organic sediments are not redistributed as in the other lakes. One possibility is that the accumulation of benthic algal biomass is greater than in the other lakes and therefore sufficient to impede the resuspension of the sediments (Holland et al. 1974; Paterson, 1989).

Conclusions

Our survey of arctic lake sediment organic matter on the Alaskan North Slope found that the surface sediments had high levels of organic matter and are accumulating substantial amounts of organic matter. Our findings further suggest that some of the variation in the organic matter content in arctic lake sediments is due to variation in benthic primary production. Our data show that variation in the organic matter content of the lake sediments occurs mainly at the lake-scale and that the percent organic matter of the shallow sediments is correlated with variation in environmental variables associated with benthic photosynthesis. We acknowledge that other factors operating at the catchment-scale can have a profound impacts on sediment organic matter and undoubtedly much of the unexplained variation in our data is related to these factors, however the significant correlation between variation in sediment organic matter, and light and oxygen, suggests that benthic photosynthesis is affecting sediment organic matter accumulation in small lakes in this region.

Consistent with what has been observed in other systems (Hobbie et al. 1980; den Heyer & Kalff, 1998; Pace & Prairie, 2005), we found that organic matter losses from the sediment via mineralization was constrained relative to overall variation in sediment organic matter suggesting that differences among lakes are principally driven by variation in organic matter inputs rather than losses.

Acknowledgments

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Tables

Table 1. The surface area and sediment characteristics of the lakes used in the study. Catchment:Lake Area is the ratio of the catchment area to the lake area. The descriptions of the sediment characteristics come from field notes collected at the time the cores were collected. The Shallow Core Sediment and Deep Core Sediment columns in the table refer to the cores collected from the shallow and deep portions of the lake (see Table 2 for depths). Within each description, the “Surface sediments” describes the sediments just below the sediment-water interface (generally 0.5 – 2 cm), while “Deep sediment” describes the sediment below the surface sediments down to 10 cm. NA indicates that notes were not recorded for the core. No Core indicates that no core was collected from that depth in that lake.

Lake	Surface Area (ha)	Catchment:Lake Area	Shallow Core Sediment	Deep Core Sediment
E-2	0.5	120.7	NA	NA
E pond			NA	No Core
E-4	4.0	10.0	Surface sediment green and grey algal material. Deep sediment brown and grey fine.	Surface sediment orange and dark grey loose. Deep sediment green and dark grey fine.
EX 1	1.1	30.8	Surface sediment orange flocculent. Deep sediment light grey fine mud.	No Core
GTH 110	8.2	15.2		
GTH 112	2.8	9.1	Surface sediment grey flocculent. Deep sediment light grey fine mud.	Surface sediment orange flocculent with numerous chironomidae tubes. Deep sediment light grey fine mud.

GTH 114	4.0	2.7	Surface sediment orange flocculent. Deep sediment grey with visible coarse organic matter.	Surface sediment orange flocculent. Deep sediment grey with visible coarse organic matter.
GTH 156	3.3		Surface sediment green algal material. Deep sediment brown loose.	Surface sediment black and orange flocculent. Deep sediment fine black.
GTH 91	2.5	16.6		
GTH 98	6.6		Surface sediment orange flocculent. Deep sediment black fine.	No Core
N-1	4.4	6.2	NA	NA
NE-10	1.0		Surface sediments fine black and orange. Deep sediments uniform fine grey.	Uniform fine black
NE-11			Surface sediments green and black algal material. Deep sediments fine black	No Core
NE-3			Light grey and jelly-like	No Core
NE-8			NA	No Core
NE-9			Sediment surface orange, flocculent. Deep sediments fine black.	No Core
NE-9b			No Core	Uniform fine black
S-10			No Core	Surface sediment black and orange flocculent. Deep sediment light grey fine.
S-11	0.4	83.0	Surface sediment black and orange flocculent. Deep sediment grey fine and small gravel.	Black and orange flocculent.
S-3	4.0	19.9	NA	NA
S-6	1.1	964.0	Green and black algal material.	Surface sediment black

		and orange flocculent. Deep sediment black flocculent.
S-7	Green and black algal material.	No Core

Table 2. Environmental data from the lakes with shallow samples in 2007 and 2008. Year refers to the year the samples were collected. Depth is the depth of the overlying water from which the sediment or water sample was collected (m). Water Temp. is the temperature of the water at the depth indicated (^{o} C). DO is the dissolved oxygen concentration of the water at the depth indicated (mg L^{-1}). Perc. Irradiance is the percent of surface photosynthetic photon flux density reaching the depth indicated. DOC is the dissolved organic carbon concentration of the water at the indicated depth (mg L^{-1}). Mean Perc. OM is the mean percent organic matter of the 10 cm core. Surf. Perc. OM is the percent organic matter of the sediments near the sediment water interface (0 - 1 cm). Missing data is indicated with a ”-”.

Lake	Year	Depth	Water Temp.	DO	Perc. Irradiance	DOC	Mean Perc. OM	Surf. Perc. OM
E-2	2007	2.2	14.4	9.2	-	-	31.2	36.6
		4.8	6.8	4.4	-	-	37.6	42.2
E pond	2007	2.1	15.6	8.0	-	-	43.5	47.0
E-4	2008	2.0	10.1	7.4	11.8	-	30.6	43.6
E-4	2008	4.0	10.2	7.4	4.4	-	39.9	42.0
EX 1	2007	2.5	10.4	-	2.4	11.1	18.5	22.6
GTH 110	2007	2.0	-	-	-	7.7	17.2	20.9
GTH 112	2007	2.0	13.6	6.3	0.4	11.5	17.4	18.2
		5.0	8.6	1.4	0.0	21.1	19.6	21.1
GTH 114	2007	2.4	13.1	8.4	9.6	8.4	25.1	30.0
		6.5	6.5	5.6	0.2	6.2	29.2	33.1
GTH 156	2007	2.0	14.5	8.3	25.7	6.1	45.5	50.3
		4.0	14.3	7.9	12.0	6.1	47.0	56.0

GTH 91	2008	3.0	10.5	-	5.4	-	23.3	28.2
		9.9	4.6	-	0.0	-	23.1	26.9
GTH 98	2007	2.4	-	-	-	5.5	25.6	51.7
N-1	2007	2.0	14.0	10.0	30.0	5.0	53.0	62.6
		22.9	3.5	7.1	0.0	5.0	35.6	40.4
NE-10	2007	2.6	10.6	8.7	5.5	-	53.2	54.6
		4.0	7.9	6.1	1.1	-	50.3	47.1
NE-11	2007	2.0	15.1	10.0	57.0	11.0	68.9	74.3
NE-3	2007	3.5	6.6	13.3	-	7.8	57.5	54.9
NE-8	2007	1.5	-	-	-	8.6	62.7	64.4
NE-9	2007	2.0	17.3	10.7	-	10.5	62.3	56.6
NE-9b	2007	7.0	3.5	0.7	0.1	9.7	51.0	52.0
S-10	2007	5.1	6.0	8.1	0.0	-	31.0	36.0
S-11	2007	4.9	6.2	7.3	12.4	-	20.4	57.9
		10.9	4.0	2.6	0.0	-	36.8	40.3
S-3	2008	2.0	9.1	-	20.9	-	66.4	73.0
		5.5	9.0	-	2.9	-	42.2	42.9
S-6	2007	2.0	17.1	-	30.8	7.6	41.6	52.7
		7.2	5.7	-	0.0	7.9	43.1	48.4
S-7	2007	2.7	16.0	-	15.1	3.8	47.8	48.9

Table 3. Results of the ^{210}Pb analysis on cores from Lakes E-4, S-3, and GTH 91. Depth indicates the water depth where the core was collected, which was the deepest location in the lake. Bulk Density is the mean (+ range) dry bulk density of the sediments (mg cm^{-3}). Sediment Accumulation Rate is the mean (+ range) estimated rate of sediment accumulation in the lake based on the distribution of ^{210}Pb in the cores (mg cm^{-2} y^{-1}) the estimates have an error of $\pm$ 10%. Sediment Accumulation Time is the mean (+ range) estimate of the number of years required to accumulate a 10 cm core (see methods for details). OM loss is the loss of percent organic matter estimated from the rate of change in percent organic matter with sediment depth and the age of the sediments in the core (% organic matter y^{-1}). NS indicates a rate that is not significantly different from 0.

Lake	Year	Depth	Bulk Density	Sediment Accumulation Rate	Sediment Accumulation Time	OM Loss Rate
E-4	2008	4.0	72.7 (62.8 – 80.0)	12.00	62.2 57.6 – 66.7)	-0.16
S-3	2008	5.5	74.3 (71.7 – 77.8)	6.09	120.8 117.7 – 123.4)	-0.17
GTH 91	2008	9.9	127.4 (122.2 – 133.5)	8.11	146.6 135.6 – 155.9)	NS

Figure Legends

Figure 1: Location of the study lakes. Lake GTH 156 is not shown but is located approximately 12.9 km north of Toolik Lake.

Figure 2: Surface percent organic matter by mean percent organic matter of the deep and shallow sediment samples. Each point represents a shallow or deep sample taken from a single lake and the line indicates a 1:1 relationship. Lakes S–11 and GTH 98 are indicated because they appear as exceptions to the general trend.

Figure 3: Mean percent organic matter of the deep sample by the mean percent organic matter of the shallow sample. Each point represents a single lake and the line indicates a 1:1 relationship. Lakes S–3 and N–1 are indicated because they appear as exceptions to the general trend.

Figure 4: The relationship between the mean percent organic matter in the sediments and the dissolved oxygen concentration of the water overlying the sediments or the percent of surface irradiance reaching the sediments. Mean percent organic matter was significantly correlated with both dissolved oxygen concentration ($r = 0.74$, $df = 11$, $p = 0.006$) and percent surface irradiance ($r = 0.73$, $df = 11$, $p = 0.004$).

Figure 5: Depth profiles of excess ^{210}Pb (open circles) and percent organic matter (closed circles) in lakes E–4, S–3 and GTH 91. The data are shown as the percent maximum value recorded, so that they could be plotted on the same figure. The maximum excess ^{210}Pb in lakes E-4, S-3, and GTH 91 was

25.0, 17.7, and 26.0 dpm g^{-1}, respectively. Each open circle is the value determined from combining 2 replicate cores from the deepest point in the lake. Each closed circle is the percent organic matter measured in one of three replicate cores collected simultaneously with the cores used for the determination of excess ^{210}Pb. The maximum percent organic matter in lakes E-4, S-3, and GTH 91 was 59.7, 46.4, and 28.5%, respectively.

Literature Cited

Appleby, P. G. & F. Oldfield, 1992. Uranium series disequilibrium: Application to Earth, Marine and Environmental Science in Application of lead-210 to sedimentation studies, pp. 731–783. Oxford Science Publications.

Ask, J., J. Karlsson, L. Persson, P. Ask, P. Byström, & M. Jansson, 2009. Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. Limnology and Oceanography 54, 2034–2040.

Beaty, S. R. K. Fortino, & A. E. Hershey, 2006. Distribution and growth of benthic macroinvertebrates among different patch types of the littoral zone of two arctic lakes. Freshwater Biology 51, 2347-2361.

Bjork-Ramberg, S., 1983. Production of epipelic algae before and during lake fertilization in a subarctic lake. Holarctic Ecology 6, 349–355.

Bretz, K. A. & S. C. Whalen, 2014. Methane cycling dynamics in sediments of Alaskan Arctic Foothill lakes. Inland Waters 4, 65-78.

Burdige, D. J., 2007. Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? Chemical Reviews 107, 467–485.

Canfield, D. E., 1994. Factors influencing organic matter preservation in marine sediments. Chemical Geology 114, 315–329.

Capone, D. G. & R. P. Kiene, 1988. Comparison of microbial dynamics in marine and freshwater sediments: Contrasts in anaerobic carbon catabolism. Limnology and Oceanography 33, 725–749.

Cole, J. J., Y. T. Prairie, N. T. Caraco, W. H. McDowell, L. T. Tranvik, R. G. Striegl, C. M. Duartie, P. Kortelainen, J. A. Downing, J. J. Middelburg, & J. Melack, 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems 10, 171–184.

Cornwell, J. C. & G. W. Kipphut, 1992. Biogeochemistry of manganese- and iron-rich sediments in Toolik Lake, Alaska. Hydrobiologia 240, 45–59.

den Heyer, C. & J. Kalff, 1998. Organic matter mineralization rates in sediments: A within and among lake study. Limnology and Oceanography 43, 695–705.

Fortino, K., A. E. Hershey, M. D. Keyes, & S. C. Whalen, 2009 Summer sedimentation in six shallow arctic lakes. Hydrobiologia, 621, 75–84.

Hamilton, T. D., 2003. Glacial geology of the Toolik Lake and upper Kuparuk River regions. University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks, AK.

Hansson, L. A., 1992. Factors regulating peripytic algal biomass. Limnology and Oceanography 37, 322–328.

Heathcote, A. J. & J. A. Downing, 2012. Impacts of eutrophication on carbon burial in freshwater lakes in an intensively agricultural landscape. Ecosystems 15, 60-70.

Hermanson, M. H., 1990. ^{210}Pb and ^{137}Cs chronology of sediments from small, shallow Arctic lakes. Geochimica et Cosmochimica Acta 54, 1443-1451.

Hobbie, J. E., T. Traaen, P. Rublee, J. P. Reed, M. C. Miller, & T. Fenchel, 1980. Limnology of Tundra Ponds in Decomposers, bacteria, and microbenthos. Dowden, Hutchensen & Ross.

Holland, A. F., R. G. Zingmark, & J. M. Dean, 1974. Quantitative evidence concerning the the stabilization of sediments by marine benthic diatoms. Marine Biology 27, 191-196.

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, & M. Jansson, 2009. Light limitation of nutrient-poor lake ecosystems. Nature, 460, 506–510.

Karlsson, J., J. Ask, & M. Jansson, 2008. Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake. Limnology and Oceanography 53, 948-954.

Livingstone, D. A., K. Bryan, & R. G. Leahy, 1958. Effects of an arctic environment on the origin and development of freshwater lakes. Limnology and Oceanography 3, 192–214.

Lovett, G. M., J. J. Cole, & M. L. Pace, 2006. Is net ecosystem production equal to ecosystem carbon accumulation? Ecosystems 9, 1–4.

Molot, L. M. & P. J. Dillon, 1996. Storage of terrestrial carbon in boreal lake sediments and evasion to the atmosphere. Global Biogeochemical Cycles 10, 483–492.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Zulueta, R. C., Hinzman, L. & Kane, D. (2000). Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature, 406, 978–981.

Pace, M. & Y. T. Prairie, 2005. Respiration in Aquatic Ecosystems in Respiration in lakes. Oxford University Press, New York, NY.

Paterson, D. M. 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnology and Oceanography 34, 223-234.

Ping, C. L., J. G. Bockheim, J. M. Kimble, G. J.Michaelson, & D. A. Walker, 1998) Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. J. Journal of Geophysical Research 103, 28917–28928.

R Development Core Team 2009. *R:* A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Stanley, D. W. 1976a. Productivity of Epipelic Algae in Tundra Ponds and a Lake near Barrow, Alaska. Ecology, 57, 1015–1024.

Stanley, D. W. 1976b. A Carbon Flow Model of Epipelic Algal Productivity in Alaskan Tundra Ponds. Ecology, 57, 1034–1042.

Tranvik, L. J., J. A. Downing, J. B. Cotner, S. A. Loiselle, R. G. Striegle, T. J. Ballatore, P. Dillon, K. Finlay, K. Fortino, L. B. Knoll, P. L. Kortelainen, T. Kutser, S. Larsen, I. Laurion, D. M. Leech, S. L. McCallister, D. M. McKnight, J. M. Melack, E. Overholt, J. A. Porter, Y. Prairie, W. H. Renwick, F. Roland, B. S. Sherman, D. W. Schindler, S. Sobek, A. Tremblay, M. J. Vanni, A. M. Verschoor, E. von Wachenfeldt, & G. S. Weyhenmeyer, 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54, 2298-2314.

Vadeboncoeur, Y., D. M. Lodge, & S. R. Carpenter, 2001. Whole-lake fertilization effects on the distribution of primary production between benthic and pelagic habitats. Ecology 82, 1065–1077.

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden, & J. Kalff, J. 2008. Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. Ecology, 89, 2542–2552.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. Academic Press, Orlando, FL.

Wetzel, R. G. & G. E. Likens, 2000. Limnological Analyses. Springer-Verlag, New York, NY.

Whalen, S. C., B. A. Chalfant, & E. N. Fischer, 2008. Epipelic and pelagic primary production in Alaskan Arctic lakes of varying depth. Hydrobiologia, 614, 243–257.

Whalen, S. C., B. A. Chalfant, E. N. Fischer, K. Fortino, & A. E. Hershey, 2006. Comparative influence of resuspended glacial sediment on physiochemical characteristics and primary production in two arctic lakes. Aquatic Sciences 68, 65-77.

Whalen, S. C. , D. D. Lofton, G. E. McGowan, & A. Strohm, 2013. Microphytobenthos in shallow arctic lakes: Fine-scale distribution of chlorophyll a, radiocarbon assimilation, irradiance, and dissolved O-2. Arctic Antarctic and Alpine Research 45, 285-295.

Figure 1

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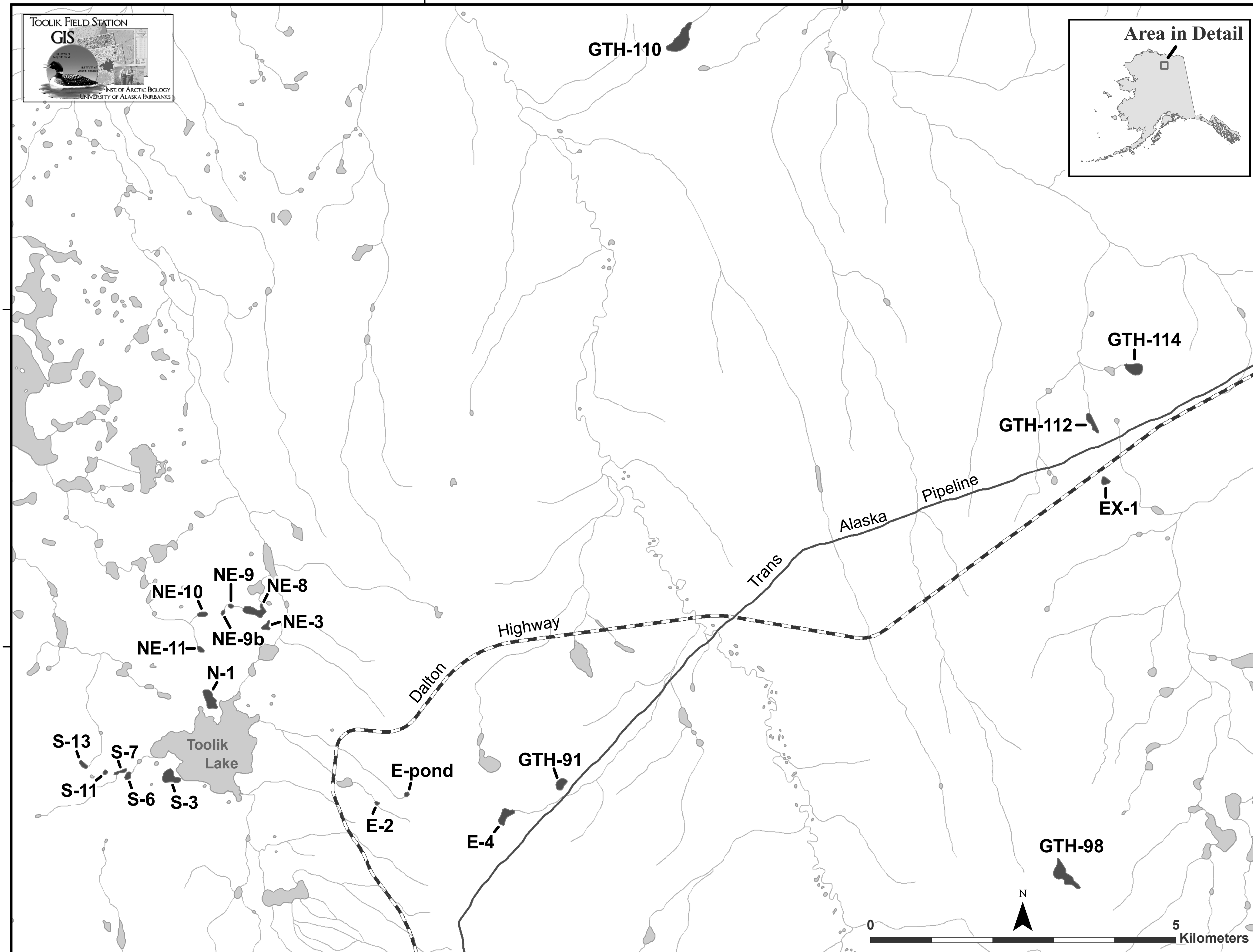

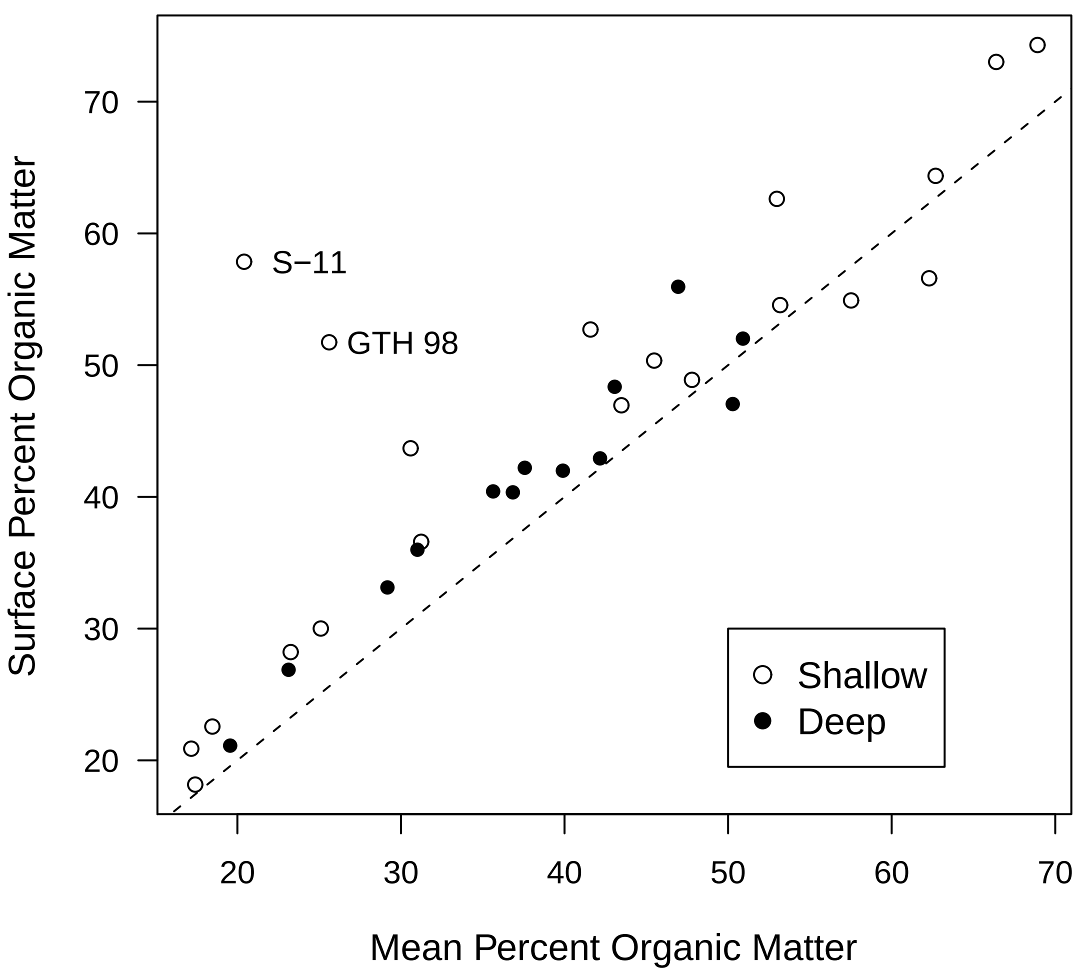

Surface Percent Organic Matter
Mean Percent Organic Matter
20
30
40
50
60
70
S−11
GTH 98
Shallow
Deep

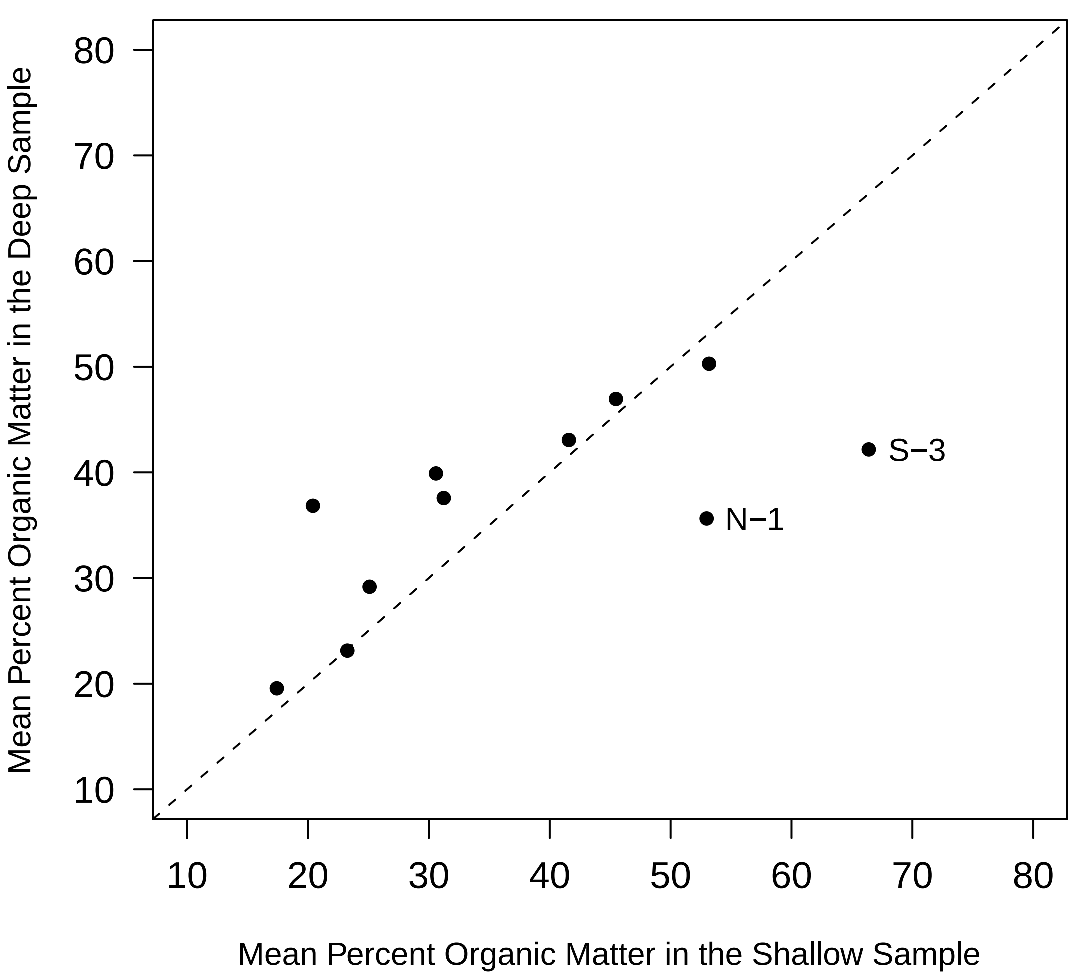
Mean Percent Organic Matter in the Deep Sample
Mean Percent Organic Matter in the Shallow Sample
S−3
N−1
10
20
30
40
50
60
70
80

Figure 4

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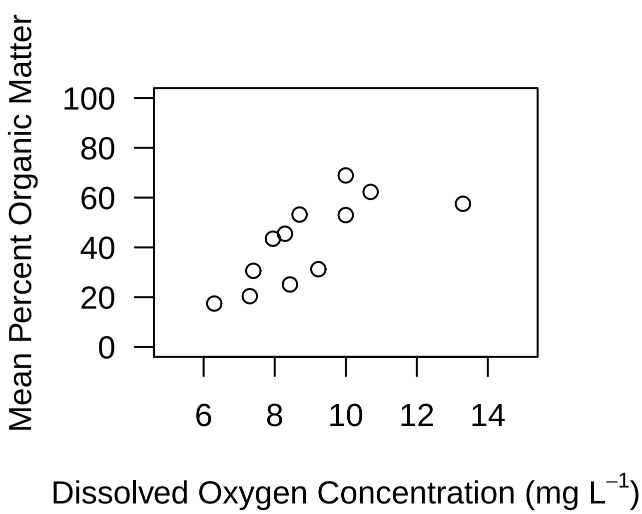


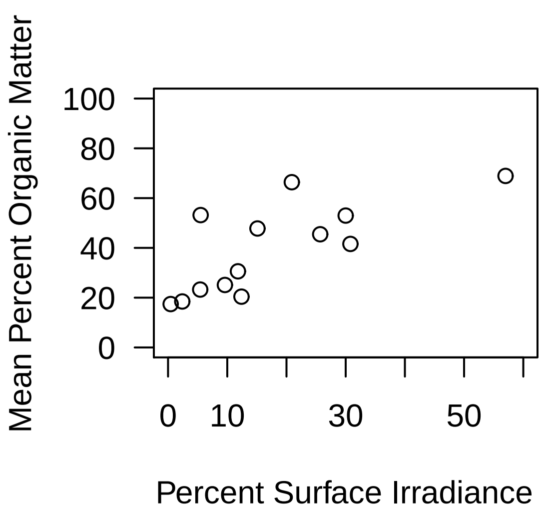
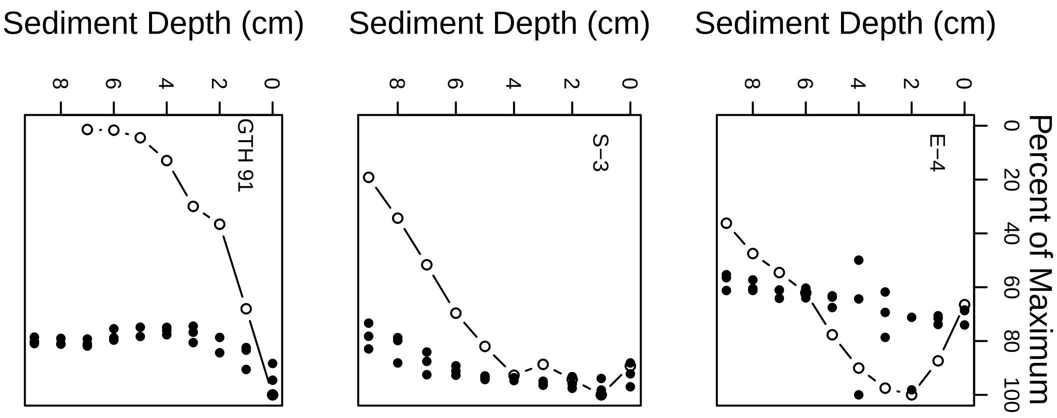


Figure 5


Sediment Depth (cm)
Sediment Depth (cm)
Sediment Depth (cm)
0 2 4 6 8
GTH 91
S–3
E–4
Percent of Maximum
0 20 40 60 80 100